VEGETATIVE REGENERATION

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Aspen is noted for its ability to regenerate vegetatively by adventitious shoots or suckers that arise on its long lateral roots. It also produces sprouts from stumps and root collars; but they are not common. In a survey of regeneration after clearcutting mature aspen in Utah, Baker (1918b) found that 92% of the shoots originated from roots, 7% from root collars, and 1% from stumps. Stump and root collar sprouts are more common when sapling-sized or younger aspen are cut; but even then, they probably do not exceed 20% of the regeneration (Maini 1968).

Origin of Suckers

Biological Development

Aspen root suckers develop from meristems that begin in the cork cambium anytime during secondary growth (Brown 1935, Sandberg 1951, Schier 1973c). This contrasts with balsam and black poplars, where most buds originate in the pericyle zone during early life of the root (Schier and Campbell 1976). These meristems may develop into buds and then elongate into shoots; but frequently, growth is arrested at the primordial stage or after a bud forms. When the stems in a clone are cut, suckers arise from new or preexisting meristems (buds and primordia) on the roots. At the same time that shoots are developing, the vascular strand is extending, by dedifferentiation of bark tissue, to the root cambium. Eventually, vascular connections are established between the shoot and the parent root.

Many thousands of suppressed shoot primordia can be found on the roots of most aspen clones. They occur as small mounds protruding from the cork cambium (Schier 1973b), and can be seen without magnification by peeling off the cork (fig. 1). Primordia occur in various stages of ontogeny—from those that are essentially small masses of meristematic cells with no tissue differentiation, to those in which procambium and protoxylem elements have been differentiated. The length of time an adventitious meristem remains in the primordial stage is unknown.

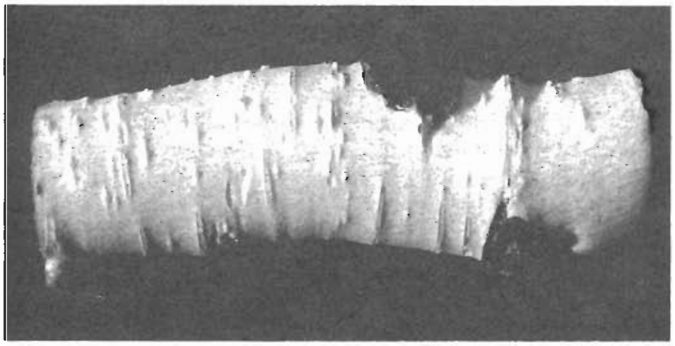

Figure 1.—The cork has been peeled away to uncover preexisting primordia on the surface of an aspen root.

Buds that have been suppressed for more than 1 year have vascular traces that extend into the secondary xylem. They grow enough each year to keep pace with the radially increasing cambium. Buds occasionally emerge as short shoots and then remain dormant for several years before developing into long shoots above the ground (Sandberg 1951). The year a bud has formed can be determined by locating the annual ring in the secondary xylem where the vascular trace originated.

Buds are not as important a source of suckers as are newly initiated meristems or preexisting primordia (Sandberg 1951, Schier 1973b). Sandberg (1951) observed that suppressed buds on roots often remained inhibited while numerous newly initiated meristems and preexisting primordia on the same root developed into suckers. In addition, suckers that originated from suppressed buds elongated much less vigorously than suckers recently initiated from meristems or primordia.

Parent Roots

Aspen root suckering is affected by the depth and diameter of the parent roots. On study areas in Utah and Wyoming, Schier and Campbell (1978a) found that 25% of all suckers arose from roots within 1.6 inches (4 cm) of the surface, 70% within 3.2 inches (8 cm), and 92% within 4.7 inches (12 cm) (fig. 2). The maximum depth of parent roots was 11 inches (28 cm). Compared with parent roots of aspen in the Lake States, those of aspen in the West were deeper. On burned areas, high burn severities increased the depth of the parent roots from which suckers were initiated.

In their study of parent roots of aspen suckers, Schier and Campbell (1978a) found that the range in diameter of roots producing suckers was 0.04 to 3.7 inches (0.1 cm to 9 cm) (fig. 3). On a Utah site, 60% of the suckers grew from roots smaller than 0.4 inch (1 cm) in diameter, 88% from roots smaller than 0.8 inch (2 cm) in diameter, and 93% from roots smaller than 1.2 inches (3 cm) in diameter. On a Wyoming site, the percentages were 38%, 68%, and 86%, respectively.

Factors Affecting Suckering

Apical Dominance

Sucker development on aspen roots appears to be suppressed by auxin transported from aerial parts of the tree (Eliasson 1971b, 1971c; Farmer 1962a, 1962b; Schier 1973d, 1975b; Steneker 1974). This phenomenon is termed "apical dominance." When movement of auxin into roots is halted or reduced by cutting, burning, girdling, or defoliation of the trees, auxin levels in the roots decline rapidly (Eliasson 1971c, 1972). This permits new suckers to begin; it also allows preexisting primordia, buds, and shoots, whose growth had been suppressed by auxin, to resume growth.

Deteriorating, overmature aspen clones often fail to regenerate because apical dominance is maintained over a shrinking root system (Schier 1975a).

Apical dominance also is important in limiting regeneration after an aspen stand is cut or burned. Elongating suckers produce auxins whose translocation into the root inhibits the initiation and development of additional suckers (Eliasson 1971a, Schier 1972).

The relatively large number of suckers that arise regularly in many undisturbed aspen clones indicates that apical dominance is not absolute (Schier 1975b, Schier and Smith 1979). This is not surprising, because auxin is a relatively unstable compound that must be transported a considerable distance from its source in developing buds and young leaves to the roots for it to have its effects. Apical dominance weakens as auxin travels down the stem because of immobilization, destruction, and age (Thimann 1977).

During normal seasonal tree growth, there are periods when apical dominance is weak enough to permit suckering. For example, in spring, before bud burst and translocation of auxin to the roots, temperatures often are high enough for suckers to begin and grow (Schier 1978c). Sucker formation is inhibited later, after the leaf buds open and apical dominance is reasserted.

Hormonal Growth Promoters

Factors stimulating root sucker initiation and growth have not been as thoroughly studied as apical dominance. Research with other plants (Peterson 1975, Skene 1975), exploratory studies in aspen (Barry 1971, Schier 1981, Williams 1972), and culture of plantlets on aspen callus (Winton 1968, Wolter 1968) all indicate that cytokinins synthesized in root meristems are involved in suckering. High ratios of cytokinins to auxins favor shoot initiation; low ratios inhibit it (Winton 1968, Wolter 1968). Changes in these ratios occur when an aspen tree is cut, because auxins no longer move into the roots, and cytokinins no longer move out of them.

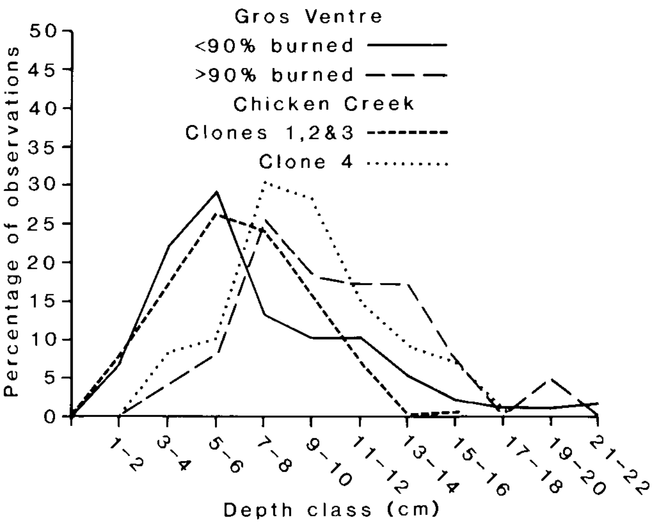

Figure 2.—Frequency distribution of root suckers in relation to parent root depth after burning in the Gros Ventre area in Wyoming and clearcutting in the Chicken Creek Watersheds in Utah (Schier and Campbell 1978a).

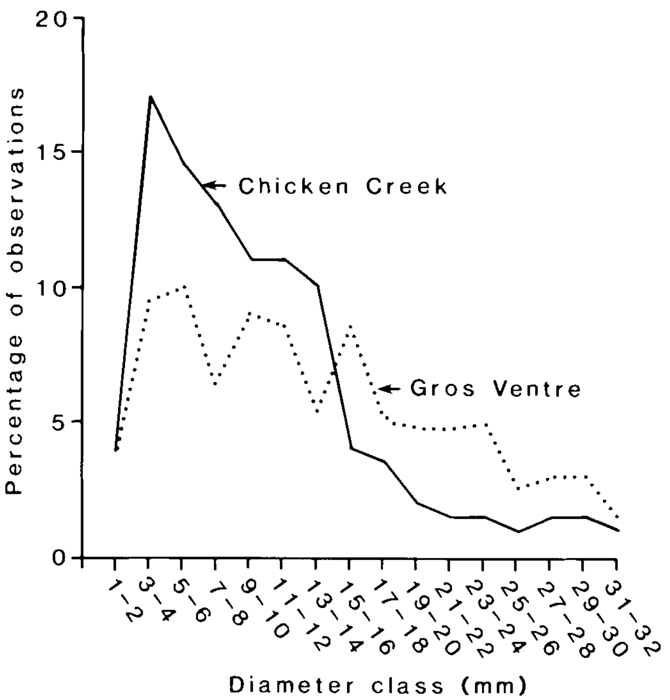

Figure 3.—Frequency distribution of root suckers in relation to parent root diameter after burning in the Gros Ventre area in Wyoming and clearcutting in the Chicken Creek Watersheds in Utah (Schier and Campbell 1978a).

Another growth regulator, a compound resembling gibberellic acid, appears to promote sucker production by stimulating shoot elongation after suckers have begun (Schier 1973a, Schier et al. 1974). Therefore, interference with its biosynthesis can reduce regeneration, even if cytokinin concentrations are high.

Abscisic Acid

Abscisic acid (ABA) may have a role in inhibiting sucker growth in dormant aspen. When young aspen were decapitated after going dormant in late summer, buds formed on the roots; but they did not elongate until the next spring (Schier 1978c). Regulation of dormancy generally seems to be controlled by a balance between endogenous inhibitors, such as ABA, and growth promoting substances, especially gibberellins. Dormancy is broken by low winter temperatures, which lower the inhibitor:growth-promoter ratio.

Carbohydrate Reserves

After a change in hormone balances triggers new shoots, carbohydrate reserves supply the energy necessary for bud development and shoot outgrowth. Primordia actually may be stimulated only in those areas of the root where there has been a heavy accumulation of starch (Thorpe and Murashige 1970).

An elongating sucker remains dependent upon parent root reserves until it emerges from the soil surface and can photosynthesize (Schier and Zasada 1973). The number of suckers developing on aspen roots generally is not limited by the concentration of stored carbohydrates. However, because sucker growth through the soil is sensitive to slight changes in carbohydrate concentration, the density of actual regeneration can be limited by low levels of carbohydrate reserves. Low supplies of carbohydrates might be expected to have more effect on regeneration from clones whose horizontal roots are deeper, because their suckers require more energy to push through to the soil surface.

After the parent stand has been removed, repeated destruction of the new suckers (such as by repeated browsing, cutting, burning, or herbicide spraying) can exhaust carbohydrate reserves and drastically reduce production of more suckers (Baker 1918b, Sampson 1919). This accounts for the dwindling sucker production on heavily browsed cutovers.

Environmental Factors

Soil temperature is important to suckering (Maini and Horton 1966b, Zasada and Schier 1973) and may account for sucker invasions of grassland adjacent to aspen stands (Bailey and Wroe 1974, Maini 1960, Williams 1972). High temperatures increase cytokinin production by root meristems (Williams 1972) and may also lower auxin concentrations in roots by speeding its degradation. The effect is a higher ratio of cytokinins to auxins, which stimulates suckering, as noted previously.

Root cuttings in a medium that is either very dry or saturated with water produce few suckers. Sucker production in the forest, however, is not inhibited by dry surface soils, because water is translocated upward through parent roots from moist soil deeper in the profile (Gifford 1964). (See the EFFECTS OF WATER AND TEMPERATURE chapter.)

Although light is not essential for sucker initiation, it is necessary for good sucker growth (Farmer 1963a). Baker (1925) compared the number of suckers under various light intensities. He found that under full sunlight in clearcuts, there were 40,000 suckers per acre (98,840 per ha). Where shading from residual aspen reduced light intensity to 50% of full sunlight or less, the number of suckers decreased to fewer than 3,000 stems per acre (7,400 per ha). (See the OTHER PHYSICAL FACTORS chapter for a more detailed discussion of the effects of light on aspen regeneration.)

Potential Sucker Production

The potential for suckering is enormous. Almost any segment of an aspen root, except newly formed root parts, can sucker under favorable conditions (Sandberg 1951). Schier and Campbell (1980) found that under artificial conditions, the number of suckers produced from 1/4- to 1/2-inch (0.6-cm to 1.3-cm) diameter root cuttings of 20 Utah aspen clones was 0.25 to 15.7 per lineal inch (0.1 per cm to 6.2 per cm); the mean number was 2.0 per inch (0.8 per cm). Barry and Sachs (1968) found a maximum of 600 sucker buds on an 18-inch-long (45-cm) root segment of 1/2-inch (1.3 cm) diameter.

Clearcutting the aspen overstory usually results in profuse, relatively rapid aspen suckering. In southwestern Colorado, commercial clearcutting of mature quaking aspen on blocks ranging from 3 to 17 acres (1 ha to 7 ha) resulted in 31,000 sprouts per acre (76,600 per ha) 1 year after clearcutting, compared to the 1,000 per acre (2,500 per ha) on the uncut blocks (Crouch 1983). In a northwestern Colorado study, clearcutting mature aspen on 5-acre (2-ha) blocks resulted in 18,000 sprouts per acre (44,500 per ha) compared to 531 stems per acre (1,300 per ha) before clearcutting (Crouch 1981). In a northern Utah study (Bartos and Mueggler 1982), the number of suckers per acre increased nearly twentyfold 2 years after clearcutting (fig. 4). Similar large increases in numbers of suckers after clearcutting were reported in other studies (Baker 1925, Hittenrauch 1976, Jones 1975, Mueggler and Bartos 1977, Sampson 1919, Smith et al. 1972). One reason for such large numbers of suckers is that they often emerge in clumps from a single point of origin on the parent root (Benson and Einspahr 1972, Sandberg 1951, Smith et al. 1972, Turlo 1963).

Jones (1976) indicated that 20,000-30,000 suckers per acre (49,400-74,100 per ha) is not excessive, because early natural thinning is heavy and effective. The number of suckers rapidly declines when suckers are

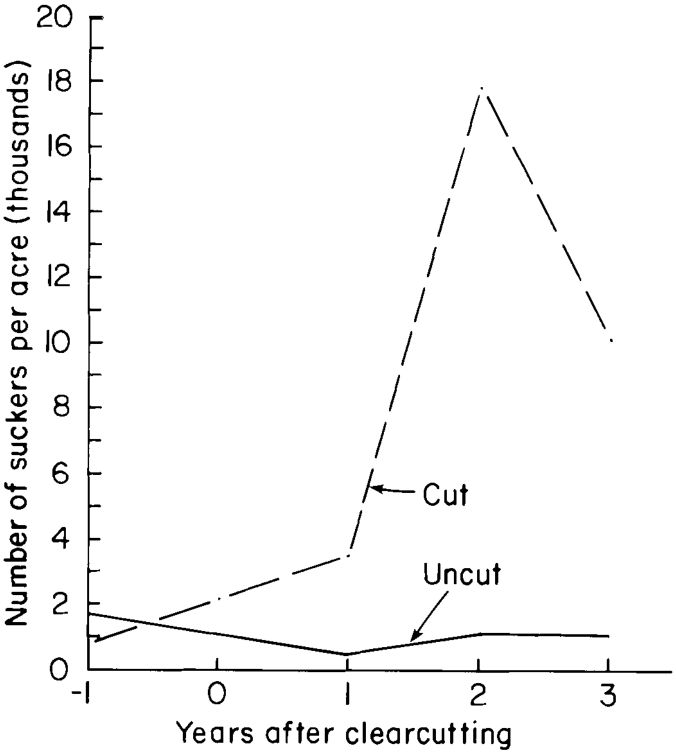

Figure 4.—Changes in the number of aspen suckers per acre on clearcut and uncut control areas from 1 year before cutting to 3 years after cutting (data from Bartos and Mueggler 1982).

extremely numerous after clearcutting (fig. 4) (Baker 1925; Bartos and Mueggler 1982; Crouch 1981, 1983; Sampson 1919; Smith et al. 1972). The least vigorous suckers die during the first 1-2 years, leaving one or two dominant suckers in each clump. Competition reduces most clumps to a single stem by the fifth year after cutting, and almost all to a single stem by the tenth year (Sandberg 1951, Turlo 1963). Competition also is a major factor in thinning out young stands of suckers. As stands develop, some of the trees become overtopped and die off (Jones 1976, Moir 1969). Diseases, insects and other invertebrates, mammals, and snow damage (Crouch 1983) also are factors (see the related chapters in PART II. ECOLOGY).

Sucker production also is affected by the stocking of the parent stand before cutting. Poorly stocked aspen produce few suckers after logging, because they do not have the necessary root densities. In Michigan, Graham et al. (1963) found the following relationship between the basal area per acre of parent stands and mean sucker production 1 year after clearcutting: less than 50 square feet, 5,200 suckers per acre (12,850 per ha); 51 to 100 square feet, 7,000 suckers per acre (17,300 per ha); and more than 100 square feet, 9,900 suckers per acre (24,450 per ha).

Where aspen stocking is low, sucker production sometimes may not peak until several years after cutting or burning. On a mixed conifer burn in New Mexico, number of suckers from the intermixed aspens increased from 11,800 stems per acre (29,150 per ha) 1 year after the fire to 14,500 stems per acre (35,800 per ha) 3 years afterwards (Patton and Avant 1970).

Occasionally, heavily cut aspen stands in Colorado produced few suckers (Hessel 1976).[1] This also has been observed in the Lake States (Fralish and Loucks 1967, Stoeckeler and Macon 1956). In some of these cases, heavy and repeated deer browsing of young suckers may have been responsible.

The failure of aspen to regenerate also has been observed in deteriorating aspen clones where production of suckers is often insufficient to replace overstory mortality (Schier 1975a). On many sites, these clones are rapidly replaced by conifers. Dry sites, however, revert to rangeland dominated by shrubs, forbs, and grasses.

Although there may be only a few scattered residual aspen in coniferous stands, aspen root suckers generally will dominate the regeneration after logging or fire if aspen root density is adequate (fig. 5). Often, the residual aspen are large veterans surviving from a time of aspen dominance (fig. 6). However, in other coniferous stands, aspens are so few they might escape casual observation (Marr 1961). On Colorado spruce-fir burns occupied by aspen stands, aspen often had been represented only sparingly before the fires (Stahelin 1943). After the fires, aspen suckers formed patches around where aspen had stood previously. The patches tended to coalesce over time by the extension and suckering of roots. The resulting stands, therefore, were only broadly even-aged. Perhaps scarcity of parent trees also accounted for the 5- to 10-year age range reported by Loope and Gruell (1973) for mature aspen stands near Jackson Hole, Wyo.

Figure 5.—A 23-year-old mixed conifer burn with dense aspen. The burned-out snag in the center was a large Douglas-fir. Most of the fallen snags were Engelmann spruce and Douglas-fir. Escudilla Mountain, Apache National Forest, Arizona.

In the lower foothills of the Canadian Rockies, Horton (1956) found aspen suckers in almost every stand regardless of age, density, or species composition. Even under very dense canopies, he found weak, inconspicuous suckers, most of which probably would live only a few years. These observations suggest that, in some areas, aspen roots occasionally may persist in the absence of canopy aspen, nurtured only by transient suckers beneath the coniferous canopy.

Figure 6.—A southwestern mixed conifer stand with aspen scattered throughout. Canopy trees on this site were primarily Douglas-fir, Engelmann spruce, corkbark fir, and aspen. Harvest of nearly all the merchantable conifers (23,000 board feet per acre) resulted in widespread suckering and aspen dominance of the regeneration stand (Gottfried and Jones 1975). Apache National Forest, Arizona.

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[1] *Betters, David R. 1976. The aspen: Guidelines for decision making. Report, Routt National Forest, Rocky Mountain Region, USDA Forest Service, 100 p. Steamboat Springs, Colo.*

Variation Among and Within Clones

The number of suckers produced can vary markedly among clones (Barnes 1969, Tew 1970a). Barry and Sachs (1968) reported large differences in sucker production among California aspen clones. Similarly, the relative capacities of different clones to produce suckers varied greatly when suckers were propagated from root cuttings in controlled environments (Farmer 1962a, Maini 1967, Schier 1974, Schier and Campbell 1980, Tew 1970a, Zufa 1971). The magnitude of these differences varied with date of root collection because of variation in the seasonal trend in sucker production among clones (Schier 1973d, Schier and Campbell 1980).

The number of suckers produced by a clone probably is related to the levels of carbohydrate reserves (Schier and Johnston 1971, Tew 1970a) and hormonal growth promoters in the roots. In the West, where single clones frequently cover several acres, such clonal differences may account for large differences in the density of suckering (Jones 1975).

Genotype probably also strongly influences suckering capacity. However, nongenetic factors, such as clone history, stem age, and environmental factors could have the major influence. Some clones, despite a high suckering capacity, produce few viable suckers when propagated from root cuttings, because their excised roots are highly susceptible to decay (Schier 1981).

The fact that some clones have an all-aged stand structure indicates that, even in undisturbed stands, suckers that die can be replaced quickly by new ones (Alder 1970). Also, apical control may be so weak, or the concentration of growth promoting substances may be so high in some clones, that they sucker vigorously after the slightest disturbance.

There also is considerable variation in suckering capacity among lateral roots within an aspen clone (Schier 1978a). Intraclonal differences among roots probably are caused by differences in the physiological condition (e.g., water content, hormone levels and ratios, concentration of nutrients), which, in turn, are caused by microclimate variability and root position in the clonal root system. Temperature, an important microclimatic element noted previously, varies with soil depth and exposure to radiation. Physiological condition as controlled by root position depends upon proximity and attachment to trees of various ages and vigor. This position determines the quantity of photosynthates and auxins and other growth regulators translocated to a particular root.

There is no evidence of a gradient in suckering capacity in a segmented root; that is, cuttings from a lateral root that were taken further from the stem did not significantly differ in suckering capacity from those taken from the same root closer to the stem (Schier 1978a). This indicates that neither distance from the parent tree, nor root age regulate suckering within lateral roots.